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Are fire, soil fertility and toxicity, water availability, plant functional diversity, and litter decomposition related in a Neotropical savana?

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Abstract

Understanding how biodiversity and ecosystem functioning respond to changes in the environment is fundamental to the maintenance of ecosystem function. In realistic scenarios, the biodiversity-ecosystem functioning pathway may account for only a small share of all factors determining ecosystem function. Here, we investigated the strength to which variations in environmental characteristics in a Neotropical savanna affected functional diversity and decomposition. We sought an integrative approach, testing a number of pairwise hypotheses about how the environment, biodiversity, and functioning were linked. We used structural equation modelling to connect fire frequency, soil fertility, exchangeable aluminium, water availability, functional diversity of woody plants, tree density, tree height, and litter decomposition rates in a causal chain. We found significant effects of soil nutrients, water availability, and aluminium on functional diversity and litter decomposition. Fire did not have a significant direct effect on functional diversity or litter decomposition. However, fire was connected to both variables through soil fertility. Functional diversity did not influence rates of litter decomposition. The mediated effects that emerged from pairwise interactions are encouraging not only for predicting the functional consequences of changes in environmental variables and biodiversity, but also to caution against predictions based on only environmental or only biodiversity change.

Key-words: Brazilian cerrado; community functioning; intraspecific variability; structural equation modeling

Introduction

Understanding how organisms respond to changing environmental conditions could help to develop more effective management policies, especially regarding how disturbances and other abiotic factors should be dealt with to reduce the loss of biodiversity and function (Loreau et al. 2001). A great amount of research on the interactions between the components of the triad of abiotic factors, biological diversity, and ecosystem functioning exist, with much of this research focusing on the relationships between two components at a time (Tilman et al. 1997; Hooper et al. 2005). For instance, several studies on the relationships between biological diversity and ecosystem functioning did not quantitatively consider the influence of abiotic factors in biodiversity-functioning components (Tilman et al. 1997; Hooper and Vitousek 1997; Hector et al. 1999). Ecosystem functioning likely responds to changes in environmental conditions not only via effects on biological diversity (Chapin et al. 1997; Cardinale et al. 2000), but also via more direct pathways of effect (Grace et al. 2007; Cardinale et al. 2009; Jonsson and Wardle 2010). For example, these more direct pathways can be modulated by abiotic controls, such as resource availability, which influence ecosystem properties (Hooper et al. 2005). In realistic scenarios, the biodiversity-functioning pathway may account for only a small share of all factors determining ecosystem properties and function (Srivastava and Vellend 2005; Grace et al. 2007; Jonsson and Wardle 2010). Incorporating the effects of the environment in biodiversity-functioning research in natural communities goes one step further with the unveiling of the relative importance of all factors that contribute to ecosystem functioning, not only biodiversity (Grace et al. 2007; Cardinale et al. 2009; Jonsson and Wardle 2010).

In niche-based models of assembly, several non-exclusive mechanisms of species sorting have been identified. One of these mechanisms is environmental filtering, where abiotic forces, such as nutrient availability, water availability, and fire, filter species with

certain trait values that give them the ability to overcome the limitations imposed by the environment (Keddy 1992). Limiting similarity, another well-studied mechanism, is determined by the interactions between species, such as competition (MacArthur and Levins 1967; Fridley 2001). For instance, species with similar trait values are likely to have overlapping positions in niche space and may, thus, compete for the same resources (Fridley 2001; Kraft et al. 2008; Cornwell and Ackerly 2009). These interactions prevent the coexistence of species with too similar trait attributes and often operate with the environment to shape the distribution of traits in a community. Thus, the stronger the pressure of the environment on individuals the lower the expected diversity of functional traits (Díaz and Cabido 2001).

Species can influence ecosystem functioning in a variety of ways (Loreau et al. 2001; Hooper et al. 2005). Increasing the number of species increases the likelihood that key species for ecosystem functioning are present in the community in a process known as the selection effect (Loreau 2000). For instance, in boreal forests, plant richness and composition drive litter decomposition rates and net primary productivity, respectively (Jonsson and Wardle 2010). However, since some species may have similar roles or contribute little to ecosystem functioning, often the number of species is not a good predictor of ecosystem functioning (Wardle et al. 1997; Hooper et al. 2005). A meta-analysis including savannas, meadows, prairies, and grasslands has shown that richness seldom explains the variation in plant biomass (Grace et al. 2007). Similar results were reported for manipulated polycultures (Petchey et al. 2004). One alternative approach is to look into the diversity of functional traits. It has been suggested that communities with higher diversity of functional traits have a tendency to operate more efficiently due to higher niche complementarity, which leads to more efficient partitioning of resources (Díaz and Cabido 2001; Petchey and Gaston 2002; Hooper et al. 2005; Petchey and Gaston 2006). Also, functional diversity is expected to

account for multiple ecosystem functions as it is measured from multiple functional traits (Cadotte 2011).

Home to at least 1,000 woody species (Castro et al. 1999), the Brazilian cerrado is under constant threat as it is being destroyed to give place to commercial cultures, such as soybean, sugarcane, and African grasses for cattle ranching (Ratter et al. 1997; Durigan et al. 2007). Cerrado soils are usually acidic Oxisols, with very low concentrations of plant nutrients (Motta et al. 2002). The concentrations of aluminium, on the other hand, are often very high (Goodland and Pollard 1973). Early investigators proposed that the higher the concentration of plant nutrients and the lower the concentration aluminium, the higher the density of woody individuals (Goodland and Pollard 1973). According to this classical theory, the cerrado is a fertility gradient, with different physiognomies occurring under soils with different concentrations of plant nutrients. However, even if nutrients play an important role in the establishment of woody individuals, it is unlikely that they are the sole responsible for the striking heterogeneity of the cerrado vegetation. Some studies on soil-vegetation relationships in cerrado areas failed to corroborate the fertility gradient theory (Ruggiero et al. 2002), indicating that other soil characteristics, such as water availability (Ferreira et al. 2007; Assis et al. 2011), may be of greater importance. Evidence shows that nutrients and plant available water can, thus, act as environmental filters, favouring a limited range of trait values. For example, nutrient-poor soil favours species with sclerophyllous leaves and drought favours deep-rooted trees (Coutinho 1990). Abiotic factors are also expected to affect decomposition. For instance, soil moisture can alter the dynamic of mass loss of litter (Gartner and Cardon 2004). Climate has also been shown to explain the variation in litter decomposition rates and carbon mineralisation (Anderson 1991; Berg et al. 1993; Madritch and Cardinale 2007).

In the cerrado, as in other savannas, fire plays an primary role in determining the composition of species (Bond and Keeley 2005; Silva and Batalha 2010) and ecosystem properties. Cerrado plant species evolved with fire and are adapted to it (Coutinho 1990). For example, woody species have thick barks and subterranean meristems that insulate internal tissues from the high temperatures and allow resprouting after burnings (Gottsberger and Silberbauer-Gottsberger 1996). Fire has been shown to act as an environmental filter, promoting clustering of functional traits in woody species (Silva and Batalha 2010). Also, areas where fires are more frequent have lower total biomass than areas with less frequent fires (Cianciaruso et al. 2010). Burning events have important impact on nutrient cycling and availability in the cerrado (Coutinho 1990; Silva and Batalha 2008). After a fire, nutrients that were in the vegetation and in the organic matter in the soil are either deposited in the soil as ashes or lost by volatilisation (Coutinho 1990).

Here, we investigated the strength to which variations in abiotic factors in the cerrado affect the functional diversity of woody individuals and ecosystem functioning, directly and indirectly. We sought an integrative approach, analysing how disturbance, water availability, and soil nutrients influence the association between the diversity of functional traits and decomposition. We proposed a structural equation model (Fig. 1) that we believed was a plausible representation of the current knowledge on how our variables of interest are connected. We answered the following questions: (1) is the variation in the frequency of burnings related to the variation in the fertility of the area? (2) Is the variation in the frequency of burnings related the variation in the functional diversity of woody individuals? (3) Is the variation in the functional diversity woody individuals related to the variation in litter decomposition? (4) Is the variation in soil aluminium contents related to the variation in the functional diversity of woody individuals? (5) Is the variation in slope and altitude, which can be used as an indicator of soil water availability, related to the variations in nutrient

availability, functional diversity of woody individuals, and litter decomposition? (6) Is the variation in tree height and density related to the nutrient supply rates? Our goal was to answer these questions by proposing a model that provided a feaseable explanation of the patterns of covariance among environmental variables and woody individuals in the cerrado.

Materials and methods

Site

Covering about 133,000 ha of the Brazilian Central Plateau (17°49'-18°28'S and 52°'39'-53°10'W), Emas National Park (ENP) is one of the largest cerrado reserves. ENP is under tropical and humid climate, with a wet summer (September to May) and dry winter (June to August). Annual rainfall and mean temperature lie around 1,745 mm and 24.6°, respectively. The cerrado vegetation in the park goes from open (68.1% of its area) to closed physiognomies (25.1%). Other vegetation types, such as wet grasslands, riparian forests, and semideciduous forests cover the remaining 6.8% of the area (Ramos-Neto and Pivello 2000). ENP is one of the most important sites containing the fauna, flora, and key habitats that characterise the cerrado.

Since the prohibition of cattle farming inside the park in 1984, a fire exclusion policy was instituted. However, the accumulation of dry biomass led to the occurrence of uncontrolled wildfires every 3-4 years, burning on average 80% of ENP's total area (França et al. 2007). In 1994, a catastrophic fire burned about 95% of the park. Since then, precautions to avoid similar burnings have been taken. Preventive firebreaks are burned annually in the dry season and a fire brigade stays in ENP during this period to prevent anthropogenic fires (França et al. 2007). Nevertheless, even with these precautions, in August 2010 an anthropogenic fire burned 93% of the park's area.

Sampling

We randomly placed 100 plots, each one with 25m^2, in all accessible areas of ENP, that is, near maintenance roads. In each plot, we collected five soil samples at 5 cm depth to determine the following soil variables (see Silva and Batalha 2008 for details on chemical and physical analyses): pH, organic matter, available phosphorus, total nitrogen, exchangeable potassium, exchangeable calcium, exchangeable magnesium, exchangeable aluminium, sum of bases, base saturation, aluminium saturation, cation exchange capacity, sand content, silt content, and clay content. Since most variables presented high bivariate correlation, we kept exchangeable aluminium, total nitrogen, available phosphorus, and cation exchange capacity for subsequent analyses, reducing model complexity. These variables are commonly regarded as important for plant growth, whilst exchangeable aluminium is toxic to plants. We also measured altitude and slope as rough surrogates of water availability: in ENP, the higher the altitude and the lower the slope, the lower the water availability in deep soil layers. Even though we could have used variables that represent soil texture, like sand content, as surrogates of water availability, these variables were highly correlated with altitude. We decided to keep altitude as it is a not a percentage measure and, thus, easier to include in the model. We determined mean interval between fire events for each plot from 1984 to 2009 based on satellite images and in-field observations. We inverted this variable by multiplying it by minus one to make interpretation easier. Thus, larger values indicate more frequent burnings.

In each plot, we identified and tagged all individuals with at least 3 cm of stem diameter at the soil level. From September 2009 to January 2010, for each sampled individual, we collected the values of 10 functional traits that are relatively easy and inexpensive to measure (Cornelissen et al. 2003; Pausas and Paula 2005). These traits are surrogates of important responses of plants to environmental conditions, such as nutrient

availability, water availability, and fire, and of impacts of plants on ecosystem functioning (Cornelissen et al. 2003; Pausas and Paula 2005). The traits we measured were: (1) basal area, related to space occupation, resource uptake, total biomass, and reproductive capability; (2) height, associated with competitive vigour, fecundity, and growth after disturbance; (3) bark thickness, related to resistance to disturbance; (4) wood density, related to the capacity to store carbon and growth after disturbance; (5) leaf toughness, associated with resistance to abiotic and biotic mechanical damage; (6) leaf size, related to resistance to environmental stress; (7) specific leaf area, associated with growth and maximum photosynthetic rate, and (8-10) leaf nitrogen, phosphorus, and potassium concentration, related to maximum photosynthetic rates and nutrient stress. We used trait values for each individual to calculate an individual-based measure of functional diversity (iFD; Cianciaruso et al. 2009). Instead of taking into account mean trait values for each species, iFD considers actual trait values for all individuals sampled. Despite the increasing awareness that trait variation within populations is important for ecological processes (Crutsinger et al. 2006; Cadotte et al. 2011), few functional diversity indices can accommodate intraspecific trait variation (Schleuter et al. 2010). iFD can, thus, detect plastic responses of individuals to environmental conditions instead of assuming that all individuals of a given species are equal regarding their traits. In the cerrado, some traits can vary more within than between species (Dantas et al. 2012). Thus, selecting a measure of functional diversity that could account for this source of variability would give us a better representation of niche width and overlap. We calculated iFD values for each plot using the "treedive" function from the "vegan" package (Oksanen et al. 2010) for the R environment (R Development Core Team 2011). We standardised the trait matrix to zero mean and unit variance before all calculations.

As a surrogate of ecosystem functioning, we used litter decomposition rates, which is one of the key functions for the maintenance of communities (Sulkava and Huhta 1998) and

regulates the cycle of matter (Clark et al. 2001). In cerrado sites, decomposition rates vary according to vegetation structure, increasing from open to closed cerrado physiognomies (Cianciaruso et al. 2006; Valenti et al. 2008) due to the increased soil moisture provided by shading. Overall, litter decomposition is very slow in the cerrado. In each plot, at the corners, we placed four sets of five decomposition bags made with 1.0 mm^2 mesh. So, we had 2,000 litterbags in total. To prepare the bags, we collected recently shed leaves from woody individuals of all species occurring in areas nearby the plots, trying to represent the surrounding species composition. We cleaned all leaves with a soft brush and oven-dried them at 80°C for 24 hours. After that, we placed all leaves in a large container and thoroughly mixed them. All leaves were fairly small and, since we over-dried them beforehand, all bags had a mixture of leaves. However, we did not seek to replicate the surrouding abundances in each litterbag. Instead, we put 5 g of mixed dried leaves in each decomposition bag. We deployed them in the plots in the middle of the rainy season (January 2010), by placing the bags fully extended on the surface of bare soil. Since the composition of each litterbag could be different, we placed 4 sets of 5 bags at the corners of each plot. We had, thus, 4 subsamples per plot to address some of the variation in decomposition rates that could arise due to differences in litter material. We collected the bags after 1, 3, and 6 months, cleaned them with a soft brush, oven-dried the material at 80ºC for 24 hours, further removed adhered soil particles, and weighed them. Since we carefully cleaned the leaves and had no reason to expect significant differences in soil mineral contamination between plots, we did not combust the contents of the litterbags to assess contamination. We planned to collect one set of bags from each plot after 1, 3, 6, 9, and 12 months to calculate decomposition rates. However, a fire burned almost all the vegetation in the park about 8 months into the experiment and we lost two sets of litterbags from each plot. Hence, we calculated decomposition rates with decay data from the first three sets of litterbags following the

equation to predict mass loss: $y = ae^{-kt}$ (Wieder and Lang 1982), where *a* is the initial weight of the bags (5 g), *k* is the decomposition rate, and *t* is the time we left the bags in the field in months.

Model

We proposed a structural equation model (Shipley 2000) with our causal assumptions regarding the following variables (Fig. 1): (1) inverted mean interval between fire events; (2) exchangeable aluminium (3-5) total nitrogen, available phosphorus, and cation exchange capacity as indicators of soil fertility; (6) altitude; (7) slope; (8) iFD; (9-10) mean tree height and density per plot; and (11) litter decomposition rates. We expected that fire would have a positive effect on soil fertility since the concentrations of some nutrients increase after moderate fires due to ash deposition (Coutinho 1990; Motta et al. 2002), despite the fact that other nutrients, such as nitrogen, are more easily lost by volatilisation (Motta et al. 2002). In our model, fire was expected to be a primary driver of nutrient supply rates through its effects on soil nutrient content.

We also expected fire to have a negative effect on functional diversity and decomposition rates. Fire has been shown to be a major driver of the functional diversity of woody plants in the cerrado (Cianciaruso et al. 2010, Silva and Batalha 2010), promoting the clustering of some traits (Dantas et al. 2013). Even though plant community dynamics can determine the frequency of burning events, in Emas fire occurrence is related to the accumulation of dry biomass from the most abundant grasses (França et al. 2007). Hence, since we were interested in the effect of fire on the functional diversity of woody individuals, we expect fire to have an influence on the distribution of traits and, consequently, the functional diversity of woody plants and not the other way around. Soil microorganisms and microenvironment also respond to fire events (Erickson and White 2008), thus fire may have a more direct influence on decomposition rates.

In Emas, the water table is higher in flat terrain (França et al. 2007). Since soil water availability can tightly related to soil nutrient dynamics and species composition in the cerrado (Ruggiero et al. 2002), we expected negative influences of both slope and altitude on soil fertility, functional diversity, and decomposition rates. Similarly, the concentration of aluminium is very high in the cerrado and has been described as one of the drivers of differences in plant community structure in the cerrado (Goodland and Pollard 1973). Moreover, aluminium is related to acidic soils, which can have low bacterial biota (Fierer and Jackson 2006). We expected a negative effect of aluminium on decomposition rates.

In addition to fire, aluminium, and water availability, we expected a positive response of functional diversity to soil fertility. The cerrado vegetation has been described as a fertility gradient, with higher tree density in more fertile soils (Goodland and Pollard 1973). We expected lower competition for nutrients and higher complementarity in resource use in soils with greater nutrient availability, which would translate into a less clustered distribution of traits and, thus, more functionally diverse communities. Also, differences in nutrient availability can alter community composition (Gross and Cardinale 2007). We expect that the turnover of species and changes in abundances caused by variations in soil fertility to leave an imprint in the distribution of traits and, consequently, in the functional diversity. Higher functional diversity is expected to influence soil biota through more efficient resource use due to the variability in litter characteristics (Collins 1981; Chapman et al. 1988). Our litterbags did not necessarily capture this plot-specific variability in litter quality, but we expected that a more complemental soil biota would have a positive effect on decomposition rates nevertheless. Soil moisture and temperature can also alter the rates of litter decay (Anderson 1991), so we assessed the impact of vegetation cover on decomposition by determining the influence of mean tree height and density on litter decomposition. We expected that plots with more and taller trees to have higher soil moisture and lower temperatures.

Even though decomposition is an important source of nutrient supply, which is expected to drive community composition and ecosystem dynamics (Gross and Cardinale 2007; Cadotte et al. 2009), the effect of the frequency of burnings on soil fertility is expected to be the main determinant of the rates at which nutrients are deposited in the soil. Indeed, in Emas the occurrence of burnings closely follows rates of grass litter accumulation (Ramos-Neto and Pivello 2007). In addition, decomposition is slow in the cerrado (Vallenti et al. 2007). Thus, in the model in Fig. 1 we hypothesised that fire is at the beginning of the causal chain linking fire, soil, functional diversity, and decomposition, and not the other way round. If we had included grasses in our study, a causal link from iFD to fire would have been warranted. In Emas, grasses contribute to most of the biomass accumulated in the soil (Ramos-Neto and Pivello 2007). Moreover, in cerrado areas with higher density and taller individuals or where drought is less pronounced, a significant effect of decomposition on community assembly might be plausible. Since we believe this is not the case in Emas given the low density of woody individuals, we did not include such causal link from decomposition to iFD in our model.

Analysis

Before testing our model, we screened our data for outliers and deviations from normality in uni- and multivariate space using robust Mahalanobis distances (Filmozer et al. 2005). When data are normally distributed in multivariate space, distances are expected to follow a chi-square distribution (Filmozer et al. 2005). Then, we log-transformed all variables except total nitrogen, available phosphorus, decomposition rates, and tree height to minimise the effects of deviations from uni- and multivariate normality. After this, we screened data for variables with high multivariate collinearity by fitting several multiple regression models, each with one of our measured variables as the response and all other variables as predictors. Models with a $R^2 > 0.85$ indicated multivariate collinearity. Then, we assured that the scales

of our variances were uniform by multiplying them to constants, which helped avoiding ill-scaled covariance structures and consequent problems during estimation (Kline 2010). With data thus screened for possible sources of problems during estimation, we generated a covariance matrix from our data (Table 1). We assured that the covariance matrix was positive-definite and all variances and covariances were within bounds (Kline 2010).

To estimate the free parameters and access the fit of the structural equation model we proposed, we used maximum likelihood estimation and maximum likelihood chi-square ($ML\chi^2$), respectively. Ultimately, maximum likelihood estimation and $ML\chi^2$ provide estimates of effects, variances and disturbances, and of how well a proposed model explains the covariance structure generated from observed data. The covariance matrix, the sample size (in our case, 100 plots), and one or a few previously specified model are all that is needed to apply structural equation modelling using maximum likelihood estimation. We used the covariance matrix and proposed model as input in the package 'lavaan' (Rossel 2011) for the R environment (R Development Core Team 2011). When the differences between observed and model-implied covariance structures are small, the model has good fit (small $ML\chi^2$). Otherwise, the model has poor fit (large $ML\chi^2$), which means that the model does not properly explain how variables interact in the system. After estimation and fit, we searched for Heywood cases in the results (Kline 2010), that is, inadmissible and not interpretable solutions (for example, negative variance estimates). Finally, we repeated the analysis passing different starting values to the estimator to assure that it would converge to the same set of parameter estimates and model fit statistic every time. We fixed the variances of all exogenous variables to their observed values. Previous screening indicated linear relationships between the variables in our model.

When considering parameter estimates that were not significantly different from zero, we looked at the corresponding bivariate residual correlation to determine whether to remove

these parameters or not. We expected that some parameters would not be significant as the model we presented was complex and the hypotheses behind some of the parameters are not very well established yet. Also, we did not seek to determine cause from an observational study. The word cause is used here as SEM jargon to determine the directionality of how we expect variables to covary given current theory. Data and R code to reproduce the structural equation modelling are made available as online supplementary files.

Results

We sampled 531 woody individuals belonging to 55 species. Fabaceae and Myrtaceae were the richest families, with 10 and 9 species, respectively. The ranges of the traits were as follows: 1) basal area: 0.004-0.147 m^2; 2) height: 0.12-5.65 m; 3) bark thickness: 0.11-29.6 mm; 4) wood density: 0.006-0.943 mg mm^{-3}; 5) leaf toughness: 0.09-8.84 N; 6) leaf size: 542-13010 mm^2; 7) specific leaf area: 0.004-20.507 mm^2 mg^{-1}; 8) leaf nitrogen content: 7.32-44.85 mg g^{-1}; leaf phosphorus content: 0.21-2.60 mg g^{-1}; and 9) leaf potassium content: 1.53-24.74 mg g^{-1}. Please refer to Batalha et al. (2011) for trait means for each sampled species. Environmental variables ranged within the following values: 1) altitude: 709-884 m; 2) slope: 0.3-8.7 º; 3) available phosphorus: 1-13 mg kg^{-1}; 4) total nitrogen: 1019-2746 mg kg^{-1}; 5) cation exchange capacity: 33-387.8 mmol kg^{-1}; 6) exchangeable aluminium 5-38 mmol kg^{-1}; 7) mean interval between fires: 1.18-8 years; 8) mean tree height 0.42-3.45 m and 9) tree density 0.08-0.76 individuals m^{-2}.

The initial model (Fig. 1) had poor fit with data (MLχ^2 = 441.142; P = 0; df = 25). Even though this model did not had and acceptable fit, not all parameters were non-significant (Fig. 2). This model resulted in some high residuals, so we went ahead and removed all the non-significant parameters from the model (Fig. 2). Removing these parameters yielded a model with much better fit (MLχ^2 = 11.263; P = 0.843; df = 17) and lower residuals.

Fire had a positive effect on the latent variable fertility (fire → fertility = 0.396; Fig. 2). This result suggested that frequent burnings were related to higher nutrient availability. Fire did not directly affect iFD and decomposition; however, both variables were indirectly influenced by fire through fertility. The signals of these indirect effects were different though: larger intervals between fire events were related to less fertile soil, which increased iFD (fire → fertility → iFD = -0.165); thus, more fires resulted in lower iFD values. Furthermore, frequent burnings resulted in more fertile soils, which, in turn, resulted in quicker decomposition; thus, more fires resulted in faster decomposition (fire → fertility → decomposition = 0.124).

The coefficients describing the direct relationships of aluminium with fertility (Al ←→ fertility = 0.031; Fig. 2), iFD (Al → iFD = 0.420; Fig. 2), and decomposition (Al → decomposition = -0.343; Fig. 2) were significant. Our model suggested that higher aluminium content increased iFD values and decreased decomposition rates. There were no indirect paths involving aluminium. The effects of altitude on iFD and decomposition were non-significant, so we removed altitude from the final model. Slope had a significant effect on iFD (slope → iFD = 0.243). Plots with higher slopes had higher iFD values and faster decomposition.

Decomposition rates were not influenced by the topography, functional diversity, density, and mean height of woody individuals. Since tree density and height were not linked to any other variables, we removed them from the final model.

Discussion

Our model integrating the variables we assumed to be the major drivers of assembly and functioning in ENP and other cerrado areas offered support for some of our pairwise causal assumptions. Furthermore, combining these hypotheses in a structural equation model enabled us to reveal indirect effects between the variables representing the environment,

biodiversity, and ecosystem functioning. Our results allowed us to quantify the strength at which alterations in one variable cause alterations in all other variables in the system, providing us with a more realistic mathematical translation of current theories of how this ecosystem works. The approach we chose also permitted us to include not only variables that are generally regarded as major drivers of assembly and functioning, but also those that are specific to the cerrado. According to our model, fire was positively related to soil fertility in ENP. Fire was also related to iFD and decomposition, although indirectly. Aluminium seemed to have an influence on several aspects of the ecosystem, including complementarity of functional traits and decomposition. The slope of the plots, which is a rough estimate of water availability to plants, had a significant effect on iFD. Functional diversity, in turn, was not directly related to the rates of decay in litter. Our whole hypothesized causal structure had good fit with data as indicated by the MLχ^2 statistic (Fig. 2). We were able to demonstrate that by simultaneously considering the pairwise hypotheses of how the variables in the system were directly connected, we were able to reveal the strength and sign of indirect relationships (Fig. 2).

The effect of fire on fertility met with our predictions. Sites that burned more frequently had more plant nutrients in the soil (fire → fertility in Fig. 2). Fire transfers nutrients from the burned vegetation to the upper soil layer as ash deposition (Coutinho 1990). Moreover, during burnings, woody individuals shed their leaves, including young ones, which are then deposited around trees as litter (Rodrígues et al. 2009). Young leaves have higher nutrient concentrations than mature leaves, so premature leaf shedding and decomposition are likely to increase nutrient availability. Several nutrients have fast turnover times in the cerrado (Pivello and Coutinho 1992) and, so, even though some chemical elements are lost by volatilisation or as particles in smoke, deposition usually compensates for this loss in 1-3 years (Coutinho 1979). Pivello and Coutinho (1992) estimated that 3-year

intervals between burnings would be optimal to avoid impoverishment of the soils and maintain nutrient cycling. Slight increases in nutrients availability up to one year after moderate fires were also found in African savannas (Jensen et al. 2001) and in the cerrado (Silva and Batalha 2008). Despite the fact that we found higher nutrient availability in the soil with increasing fire frequencies, the relationships between fire, nutrients, and the vegetation are still unclear, since contrasting results have been found, even in the cerrado (Kauffman et al. 1994; Moreira 2000; Pivello et al. 2010). For instance, grass biomass is expected to have a major influence on both fire and nutrients. Thus, a covariance between both variables to account for the absence of an indicator of grass abundance might have been a better specification. Finally, aluminium and plant nutrients are likely introduced in the soil by some of the same processes mentioned above (e.g. weathering), thus the observed correlation between fertility and aluminium (fertility ← → Al in Fig. 2).

Contrarily to our expectations, the fire → iFD path was not significant. Low and moderate fire frequencies might have not been strong enough environmental filters to leave an imprint in functional diversity (Cianciaruso et al. 2012). Thus, the apparent absence of functional structuring in sites with fewer burnings might have decreased the strength of the path between fire and iFD, rendering it statistically non-significant. Also, fire possibly caused a turnover of species without causing loss of functional diversity or ecosystem function in a process known as the insurance hypothesis (Yachi and Loreau 1999; Loreau 2001). Our model might have supported the path connecting fire and iFD if we had used a different set of traits (Cianciaruso et al. 2012). However, even in the absence of a direct effect, there was a small indirect effect of fire on iFD through soil fertility (Table 2). More frequent fires promoted faster nutrient cycling which, in turn, were associated with less trait complementarity and lower iFD. Absence of trait structuring in sites with different occurrence of burnings in ENP also suggests that fire might be filtering species at the regional level, so

1 the species we sampled were already selected and local filtering by fire was not strong enough
2 determine the distribution of trait-states (Dantas et al. 2012).
3 Variations in soil chemical elements triggered a response in iFD (fertility → iFD and
4 Al → iFD paths in Fig. 2) and decomposition (fertility → decomposition and Al →
5 decomposition in Fig. 2). We observed a negative relationship between fertility and iFD
6 (fertility → iFD path in Fig. 2) and a positive one between aluminium and iFD (Al → iFD
7 path in Fig. 2). These findings strongly support the hypotheses represented in the structural
8 equation model, and highlight the importance of nutrients and aluminium for plant functional
9 diversity and ecosystem decomposition rates. In the cerrado, soil characteristics have been
10 regarded as promoters of trait clustering through environmental filtering (Batalha et al. 2011).
11 Areas with low nutrient availability may promote competitive exclusion, limiting the
12 similarity of individuals (Stubbs and Wilson 2004). This process decreases the overlap in
13 niche occupation, which might lead to higher iFD. Although low nutrient availability can
14 promote trait clustering, competition for limited resources contributes to the selection of
15 specialised nutrient and nutrient uptake requirements, imposing a force in the opposite
16 direction. Similarly, plants have several ways of circumventing the toxic effects of aluminium
17 (Kochian 1995). Thus, high concentrations of exchangeable aluminium might increase trait
18 diversity and iFD. Also, high concentrations of exchangeable aluminium are related to acidic
19 soils, which are reported to have low bacterial diversity when compared to neutral soils
20 (Fierer and Jackson 2006). Low bacterial biota might have led to slower decomposition.
21 Moreover, ants can change soil properties near their nests (Wagner et al. 1997; Frouz et al.
22 2003). Areas with ant nests nearby have more soil nutrients (Wagner et al. 1997; Frouz et al.
23 2003) and higher pH (Frouz et al. 2003), due to ant activity, so the positive link between
24 fertility and decomposition and the negative link between aluminium and decomposition in
25 our model might be related to the presence of ants. Our data did not include information on

ant activity in plots, so we could not explicitly consider and this activity in the model. Including other trophic levels into future models will certainly help clarify some of the associations in biodiversity-functioning research (Hooper et al. 2005, Srivastava and Vellend 2005). It is important to note that feedback mechanisms we not addressed due to data limitations. For example, it is likely that decomposition has some effect on iFD and on soil fertility. In order to model these feedbacks in further studies, one should track the changes in all variables with time.

In ENP, hilly terrain seemed to increase functional diversity (slope → iFD path in Fig. 2), which supported the theory that water availability is one of the most important determinants of vegetation structure in the cerrado (Ferreira et al. 2007; Assis et al. 2011). In ENP's flatland, the water table is high enough to prevent even shallow-rooted woody individuals to reach it. In hilly areas, however, the water table is deeper and favours the establishment of those woody individuals capable of reaching deep soil layers (Cole 1986; Franco 2002). Thus, in sites where there is less water available, environmental filtering might favour the occurrence of the woody layer, leading to higher functional diversity since there is less competition with the herbaceous layer for other resources, such as soil nutrients. In spite of altitude also being related to the depth of the water table in ENP, it was not one of the variables in our model with best fit.

Changes in iFD did not lead to variations in decomposition (iFD → decomposition path in Fig. 2), contrarily to our expectations. Functional traits can have great influence on ecosystem fluxes, pools, and function (Hooper et al. 2005). Higher biodiversity, especially when considering the functional component, can increase complementarity in patterns of resource use (Tilman et al. 1997; Petchey and Gaston 2002), which results in more efficient functioning. For instance, Scherer-Lorenzen (2008) found a significant positive effect of functional group diversity on decomposition in experimental grasslands. Moreover, soil biota

may be influenced by plant functional diversity and, as a consequence, influence litter decomposition (Collins 1981; Chapman et al. 1988). Similarly, tree cover might influence local moisture and temperature. However, tree density and height in our plots might not have been high enough to influence the microenvironment of the plot and trigger a response in decomposition rates. The dynamics of the herbaceous layer, which contributes with a very high amount of dry biomass and percent cover in the cerrado (França et al. 2007), might be of greater influence to litter breakdown.

Fire also did not have a direct effect on decomposition. In the cerrado, arthropods are fundamental agents of litter breakdown. The communities of several leaf-litter arthropods slightly decrease in number of individuals following a fire, but they are able to quickly recover and resume litter breakdown (Vasconcelos et al. 2009). Thus, the litter-dwelling activities of these arthropods might not have been significantly affected by burnings, which supressed any possible direct effects of fire on decomposition. Even though fire was not directly related to functioning, there was a path linking fire to decomposition through soil fertility (please refer to Table 2 for net effects).

Several aspects of the environment might alter the strength of the relationship of biotic and abiotic components, both directly and indirectly and through different pathways. We were able to identify and quantify some of the multiple paths that causally connect the environment, biodiversity, and ecosystem functioning. The causal links that are thought to be the most important for determining the biodiversity-functioning relationship can be complex. For instance, we could not identify a direct influence of fire on iFD. Fire did have, however, a strong link to soil fertility, which, in turn, helped shaping the distribution of iFD values in our plots. Similarly, we identified am indirect path between fire and decomposition through soil fertility, even though we did not find a significant direct connection. Having a better understanding of how abiotic factors interact with each other and with biodiversity and

function can uncover critical paths for the conservation of biological diversity and ecosystem function (Srivastava and Vellend 2005; Grace et al. 2007; Jonsson and Wardle 2010). If we had analysed the effects of fire on biodiversity directly, we would probably have found a non-significant relationship. However, considering soil fertility as a mediator of the fire → iFD path, we were able to uncover a strong link between these variables. Moreover, the net effects of the multiple ways in which the effects of disturbances can propagate in a causal network can be large even without the presence of a direct connection between disturbance and biodiversity (Table 2).

Soil chemical elements and water availability were the most important direct causes of change to the iFD-decomposition relationship. We detected direct effects of fertility (fertility → iFD and fertility → decomposition in Fig. 2), aluminium (Al → iFD and Al → decomposition in Fig. 2), and slope (slope → iFD in Fig. 2) on iFD. Our results also suggest that fire has an important role on the biodiversity and functioning through soil nutrients. The absence of a significant path between fire and iFD indicate that fire might be selecting traits at the regional level. It is important to note that this study was cross-sectional, so we did not try to model the feedback mechanisms of biodiversity and functioning on abiotic factors. Long-term studies with data on the fluctuations of biotic and abiotic factors in different seasons might shed light on these feedbacks. For instance, inter-year variability in litterfall was reported in island ecosystems (Wardle et al. 2012) and this could influence the relationships between the environment and ecosystem functioning. Also, modelling the multidimensionality of the biodiversity and functioning components by including more diversity indices and other ecosystem properties will yield more adequate models. Structural equation models with latent variables are appropriate tools for modelling these multidimensional concepts (for instance, fertility in Fig. 1). Furthermore, different ecosystem fluxes and properties might be affected by different sets of trait attributes, possibly changing

1 the strength and directionality of the biodiversity-functioning pathway as models become
2 more realistic. Ecosystem functioning research must address all these uncertainties to propose
3 biodiversity-functioning models that are more relevant to the conservation of biodiversity and
4 services (Hooper et al. 2005; Srivastava and Vellend 2005). Here we considered only one
5 aspect of biodiversity and functioning for one cerrado site, so one should be careful when
6 extrapolating our results for other vegetation types and areas.

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14 **References**

15 Anderson JM (1991) The effects of climate change on decomposition processes in grassland
16 and coniferous forests. Ecol Appl 1: 326-347
17 Assis ACC, Coelho RM, Pinheiro ES, Durigan G (2011). Water availability determines
18 physiognomic gradient in an area of low-fertility soils under cerrado vegetation. Plant
19 Ecol 212: 1135-1147
20 Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schimid B
21 (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and
22 services. Ecol Lett 9: 1146-1156

Batalha MA, Silva IA, Cianciaruso, MV, França H, Carvalho GH (2011) Phylogeny, traits, environment, and space in cerrado plant communities at Emas National Park (Brazil). Flora 206: 949-956

Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Couteaux M, Escudero A, Gallardo A, Kratz W, Madeira M, Mälkönen E, McClaugherty C, Meentemeyer V, Muñoz F, Piussi P, Remacle J, Virzo de Santo A (1993) Litter mass-loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemestry 20: 127-159

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20: 387-394

Cadotte MW (2011) The new diversity: management gains through insights into the functional diversity of communities. J Appl Ecol 48: 1067-1069

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48: 1079-1087

Cardinale BJ, Nelson K, Palmer MA (2000) Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos 91: 175-183

Cardinale BJ, Bennett DM, Nelson CE, Gross K (2009) Does productivity drive diversity or vice versa? A test of the multivariate productivity-diversity hypothesis in streams. Ecology 90: 1227-1241

Castro AAJF, Martins FR, Tamashiro JY, Shepherd GJ (1999) How rich is the flora of the Brazilian cerrados? Ann Mo Bot Gard 86: 192-224

Chapin, FS III, Walker BW, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. Science 277: 500-504

Chapman K, Whittacker JB, Heal OW (1988) Metabolical and faunal activity in litters of tree mixtures compared with pure stands. Agr Ecol Env 24: 33-40

Cianciaruso MV, Batalha MA, Gaston KJ, Petchey OL (2009) Including intraspecific variability in functional diversity. Ecology 90: 81-89

Cianciaruso MV, Pires JSR, Delitti WCB, Silva EFP (2006) Produção de serapilheira e decomposição do material foliar em um cerradão da Estação Ecológica de Jataí, Luiz Antônio, SP. Acta Bot Bras 20: 49-59

Cianciaruso MV, Silva IA, Batalha MA (2010) Above-ground biomass of functional groups in the herbaceous layer of savannas under different fire frequencies. Aust J Bot 58: 169-174

Cianciaruso MV, Silva IA, Batalha MA, Gaston KJ, Petchey OL (2012) The role of fire on phylogenetic and functional structure of woody savannas: moving from species to individuals. Perspect Plant Ecol 14: 205-216

Clark DA, Brown S, Kichlighter WK, Charmbers JQ, Thomlinson JR, Ni J, Holland EA (2001) Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol Appl 11: 371–384

Cole MM (1986) The savannas, biogeography and geobotany. Academic Press, London.

Collins NM (1981) The role of termites in the decomposition of wood and leaf litter in the southern Guinea savanna of Nigeria. Oecologia 51: 389-399

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, var der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51: 335-380

Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecol Monogr 79: 109-126

Coutinho LM (1979) Aspectos ecológicos do fogo no cerrado: III. A precipitação atmosférica de nutrientes minerais. Rev Bras Bot 1: 93-97

1 Coutinho LM (1990) Fire in the ecology of the Brazilian cerrado. In: Goldammer JG (eds)
2 Fire in the tropical biota. Springer, Berlin, pp 81-103
3 Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ (2006) Plant
4 genotypic diversity predicts community structure and governs ecosystem process.
5 Science 313: 966-968
6 Dantas VL, Pausas JG, Batalha MA, Loiola PP, Cianciaruso MV (2013) The role of fire in
7 structuring trait variability in neotropical savannas. Oecologia 171: 487-494
8 Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem
9 processes. Trends Ecol Evol 16: 646-655
10 Durigan G, Siqueira MF, Franco GADC (2007) Threats to the cerrado remnants of the state of
11 São Paulo, Brazil. Scientia Agricola 64: 355-363
12 Erickson HE, White R (2008) Soils under fire: soils research and the joint fire science
13 program. General Technical Report 759. US Dept of Agriculture
14 Ferreira JN, Bustamante M, Garcia-Montiel DC, Caylor KK, Davidson EA (2007) Spatial
15 variation in vegetation structure coupled to plant available water determined by two-
16 dimensional soil resistivity profiling in a Brazilian savanna. Oecologia 153: 417-430
17 Fierer N, Jackson RB (2006) The diversity and biogeography of soil microbial communities.
18 P Natl Acad Sci USA 103: 626-631
19 Filmozer P, Garret RG, Reimann C (2005) Multivariate outlier detection in exploration
20 geochemistry. Comput Geosci 31: 579-587
21 França H, Ramos-Neto MB, Setzer A (2007) O fogo no Parque Nacional das Emas.
22 Ministério do Meio Ambiente, Brasília
23 Franco AC (2002) Ecophysiology of woody plants. In: Oliveira PS, Marquis RJ (eds) The
24 cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia
25 University Press, New York, pp 178-197

Fridley JD (2001) The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93: 514-523

Frouz J, Michal H, Kalčík J (2003) The effect of *Lasius niger* (Hymenoptera, Formicidae) ant nest on selected soil chemical properties. Pedobiologia 47: 205-212

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104: 230-246

Goodland R, Pollard R (1973) The Brazilian cerrado vegetation: a fertility gradient. J Ecol 61: 219-224

Gottsberger G, Silberbauer-Gottsberger I (2006). Life in the cerrado: a South American tropical seasonal vegetation. Vol. 1. Origin, structure, dynamics and plant use. Reta, Ulm

Grace JB, Anderson TM, Smith MD, Seabloom E, Andelman SJ, Meche G, Weiher E, Allain LK, Jutila H, Sankaran M, Knops J, Ritchie M, Willig MR (2007) Does species diversity limit productivity in natural grassland communities? Ecol Lett 10: 680-689

Gross K, Cardinale BJ (2007) Does species richness drive community production of vice versa? Reconciling historical and contemporary paradigms in competitive communities. Am Nat 170: 207-220

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286: 1123-1127

1 Hooper DU, Chapin FSIII, Ewel AH, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge
2 DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA
3 (2005) Effects of biodiversity on ecosystem functioning: a consensus of current
4 knowledge. Ecol Monogr 75: 3-35
5 Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on
6 ecosystem processes. Science 277: 1302-1305
7 Jensen M, Michelsen A, Gashaw M (2001) Responses in plant, soil inorganic and microbial
8 nutrient pools to experimental fire, ash and biomass addition in a woodland savanna.
9 Oecologia 128: 85-93
10 Jonsson M, Wardle DA (2010) Structural equation modelling reveals plant-community
11 drivers of carbon storage in boreal forest ecosystems. Biol Letters 6: 116-119
12 Kauffman JB, Cummings DL, Ward DE (1994) Relationships of fire, biomass and nutrient
13 dynamics along a vegetation gradient in the Brazilian cerrado. J Ecol 82: 519-531
14 Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology.
15 J Veg Science 3: 157-164
16 Kline RB (2010) Principles and practice of structural equation modeling. Guilford, New York
17 Kochian LV (1995) Cellular mechanisms of aluminum toxicity and resistance in plants. Annu
18 Rev Plant Phys 46: 237-260
19 Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community
20 assembly in an Amazonian forest. Science 322: 580-582
21 Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos
22 91: 3-17
23 Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA,
24 Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem
25 functioning: current knowledge and future challenges. Science 294: 804-808

MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. Am nat 101: 377-385

Madritch MD, Cardinale BJ (2007) Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: a multi-site experiment along a latitudinal gradient. Plant Soil 292: 147-159

Moreira AG (2000) Effects of fire protection on savanna structure in Central Brazil. J Biogeogr 27: 1021-1029

Motta PEF, Curi N, Franzmeier DP (2002) Relation of soils and geomorphic surfaces in the Brazilian cerrado. In: Oliveira PS, Marquis RJ (eds) The cerrados of Brazil: ecology and natural history of a Neotropical savannah. Columbia University Press, New York, pp 13-32

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2010) Vegan: community ecology package. URL: http://CRAN.R-project.org/package=vegan

Pausas JG, Paula S (2005) Plant functional traits database for Euro–Mediterranean ecosystems. Eufirelab Deliverable D–04–06. URL: http//www.eufirelab.org

Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. Ecol Lett 5: 402-411

Petchey OL, Hector A, Gaston KJ (2004) How do different measures of functional diversity perform? Ecology 85: 847-857

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9: 741-758

Pivello VR, Coutinho LM (1992) Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). J Trop Ecol 8: 487-497

Pivello VR, Oliveras I, Miranda HS, Haridasan M, Sato MN, Meirelles ST (2010) Effects of fire on soil nutrient availability in an open savanna in Central Brazil. Plant Soil 337: 111-123

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: http://www.r-project.org

Ramos-Neto MB, Pivello VR (2000) Lightning fires in a Brazilian savanna national park: rethinking management strategies. Environ Manage 26: 675–684

Ratter JA, Ribeiro JF, Bridgewater S (1997) The Brazilian cerrado vegetation and threats to its biodiversity. Ann Bot 80: 223-230

Rodrígues A, Duran J, Fernández-Palacios JM, Gallardo A (2009) Short-term wildfire effects on the spatial pattern and scale of labile organic-N and inorganic-N and P pools. Forest Ecol Manag 257: 739-746

Rosseel Y (2011) lavaan: an R package for structural equation modeling. J Stat Soft 48: 1-35.

Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. Plant Ecol 160: 1-16

Scherer-Lorenzen M (2008) Functional diversity affects decomposition processes in experimental grasslands. Func Ecol 22: 547-555

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecol Monogr 80: 469-484

Shipley B (2002) Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge

Silva DM, Batalha MA (2008) Soil–vegetation relationships in cerrados under different fire frequencies. Plant Soil 311: 87–96

Silva IA, Batalha MA (2010) Woody plant species co-occurrence in Brazilian savannas under different fire frequencies. Acta Oecol 36: 85-91

Srivastava DS, Vellend M (2005) Biodiversity-ecosystem functioning research: is it relevant to conservation? Annu Rev Ecol Evol S 36: 267-294

Stubbs WJ, Wilson JB (2004) Evidence for limiting similarity in a sand dune community. J Ecol 92: 557-567

Sulkava P, Huhta V (1998) Habitat patchiness affects decomposition and faunal diversity: a microcosm experiment on forest floor. Oecologia 116: 390-396

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. P Natl Acad Sci USA 94: 1857-1861

Valenti MW, Cianciaruso MV, Batalha MA (2008) Seasonality of litterfall and leaf decomposition in a cerrado site. Braz J Biol 68: 459-465

Vasconcelos HL, Pacheco R, Silva RC, Vasconcelos PB, Lopes CT, Costa AN, Bruna EM (2009) Dynamics of the leaf-litter arthropod fauna following fire in a neotropical woodland savanna. PLoS ONE 11: e7762

Wagner D, Brown MJF, Gordon DM (1997) Harvester ant nests, soil biota and soil chemistry. Oecologia 112: 232-236

Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79: 247-258

Wardle DA, Jonsson M, Kalela-Brundin M, Lagerström A, Bardgett RD, Yeates GW, Nilsson MC (2012) Drivers of inter-year variability of plant production and decomposers across contrasting island ecosystems. Ecology 93: 521-531

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63: 1636–1642

1 Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating
2 environment: the insurance hypothesis. P Natl Acad Sci USA 96: 1463-1468